

## Climate-averaging of terrestrial faunas: an example from the Plio-Pleistocene of South Africa

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*Abstract.*—Fundamental to the interpretation of bone-bearing faunal deposits is an understanding of the taphonomic processes that have modified the once living fossil community. An often neglected source of bias is that of climate-averaging, which occurs when the duration of bone accumulation exceeds the duration of an individual climatic episode. Tropical and subtropical climate change is dominated by precessional cyclicity (~21,000 year cycle), which controls monsoon rainfall intensity and thus plant communities over time. Under a climate-averaging scenario, the paleoecological characteristics of a faunal deposit represent an amalgamation of more than one phase of the precessional cycle. We investigate the degree of climate-averaging in Plio-Pleistocene bone breccias from South Africa by comparing stable isotope measurements of fossil enamel with the evidence from high-resolution speleothem paleoclimate proxies. We conclude that each of the four faunal assemblages studied are climate-averaged, having formed over a time period in excess of one-third of a precessional cycle (~7000 years). This has implications for the reconstruction of hominin paleoenvironments and estimates of Plio-Pleistocene biodiversity. We hypothesize that climate-averaging may be a common feature of tropical terrestrial vertebrate assemblages throughout the Cenozoic and Mesozoic.

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### Introduction

Virtually all faunal assemblages have undergone a certain degree of time averaging—accumulation or mixing over time (Behrensmeyer et al. 2000)—from seasons or years to thousands or millions of years. Time-averaging can affect the interpretation of temporal events within the geological record, and is largely of concern in studies of biostratigraphy or faunal correlation. The paleoecological integrity of a faunal deposit also can be affected by time-averaging, depending principally on the duration of time-averaging in relation to the rate of paleoecological change (Behrensmeyer et al. 2007). Some paleoecological events are stepwise in nature (tsunamis, volcanic eruptions, changes in ocean circulation), whereas others are cyclical (annual variability, El-Niño southern oscillation [ENSO], and orbital forcing). Time-averaging of stepwise events leads to a dampening or loss of the paleoecological signal, whereas time-averaging of cyclical events results in a mixing of the two end-member paleoecolog-

ical states (see Fig. 1). Given the high frequency of seasonal and El Niño/La Niña cycles, the vast majority of faunal deposits have accumulated over periods of time that exceed the duration of these cycles, and the seasonal and ENSO signals are lost. In contrast, the long duration of orbital cycles (up to 100,000 years for eccentricity) has been assumed to be considerably longer than the period of time represented by most vertebrate accumulations (tens to tens of thousands of years of accumulation [Behrensmeyer et al. 2000]). However, climate change in tropical and subtropical regions is dominated by the shortest Milankovitch cycle, the ~21,000 year precessional cycle, which leads to rainfall and vegetation extremes every ~10,500 years (Clement et al. 2004; Maslin and Christensen 2007). This study makes a first attempt to evaluate the effects of such frequent and rapid climate changes on the paleoecological integrity of faunal assemblages.

Little consideration has been given to the mixing of orbital extremes within faunal

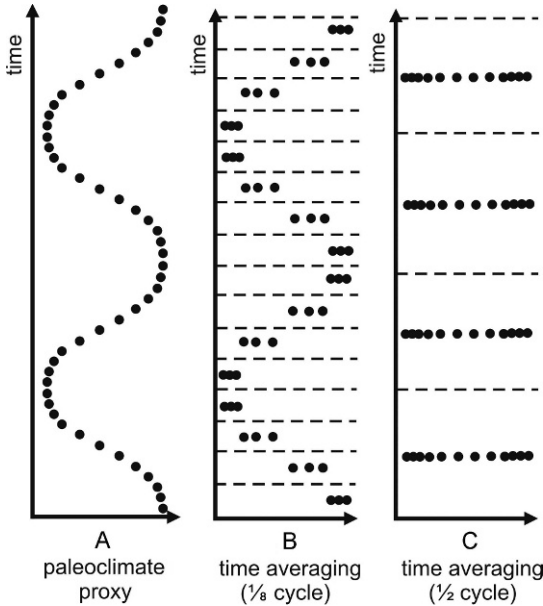


FIGURE 1. An assessment of the environmental fidelity of time-averaged faunal deposits under an oscillating climate. A, Hypothetical paleoclimate curve showing oscillations typical of orbitally forced climate change. B, Time-averaging at intervals of an eighth of a cycle preserves the key paleoclimatic information. C, Time-averaging at intervals of half a cycle obscures the oscillatory nature of the paleoclimate proxy. In this scenario, inter-assemblage variability is minimal and intra-assemblage variability is high. Each assemblage in C exhibits a bimodal distribution.

assemblages, perhaps owing to the unfounded assumption that these cycles are too long to affect the paleoecological integrity of a faunal assemblage. We therefore introduce the term “climate-averaging” to document the amalgamation of individuals living under one or more climatic states within a single faunal deposit. We suggest that as a concept, climate-averaging is as important to paleoecological analysis as time-averaging is to biostratigraphy or faunal correlation. Because most cyclical climatic events have known frequencies, investigations of climate-averaging can potentially provide some constraint on the amount of time represented by a faunal assemblage.

One approach to the climate-averaging problem is to use a comparative paleoclimatic data set that is independent of the faunal assemblage in question. Such a data set must overlap geographically and temporally with the faunal assemblage and should consist of equivalent proxy data. Paired paleoclimate

archives from faunal and geological sources are rare in the Mesozoic and Cenozoic, however the Plio-Pleistocene of Africa is a notable exception. In recent decades a large body of work, based on faunal analysis (abundance analysis, ecomorphology, stable isotopes) and sedimentology (stable isotopes, stratigraphic studies), has produced numerous detailed paleoecological data sets from hominin localities (e.g., Kingston 2007). These data sets provide the opportunity for an initial investigation of climate-averaging in low-latitude terrestrial assemblages.

### Hominin Palaeoecology and Time-Averaging

Understanding the environmental context of human evolution in Africa has become a focus of paleoanthropological research (Behrensmeyer 2006). Paleoenvironmental studies can provide insights into early hominin ecology (sympatry, predator/prey relationships), adaptations such as diet and locomotion, and evolutionary processes such as speciation and extinction events. Paleoenvironmental evidence is sourced from a variety of Plio-Pleistocene data sets ranging in scale from global to regional to site-specific (Kingston 2007). Faunal assemblages are the principal source of paleoecological and paleoclimatic information, specifically at the local scale (Kingston 2007). Temporal constraints are provided by radiometric or relative dating, and typically have age uncertainties of  $>10^5$  years. Such low temporal resolution offers insights into gradual ecosystem evolution but cannot resolve orbitally forced climate change, which occurs at time scales of  $>10^4$  years. Although various studies have demonstrated that modern faunal assemblages can have geographical integrity (e.g., Kovarovic and Andrews 2007; Plummer et al. 2008), only limited consideration has been given to the temporal integrity of paleoecological archives. In this study we investigate the paleoecological integrity of faunal deposits with respect to orbitally forced climate change, with particular focus on South African Plio-Pleistocene cave deposits (see Fig. 2).

The bone-bearing breccia deposits from the Plio-Pleistocene of South Africa have been the

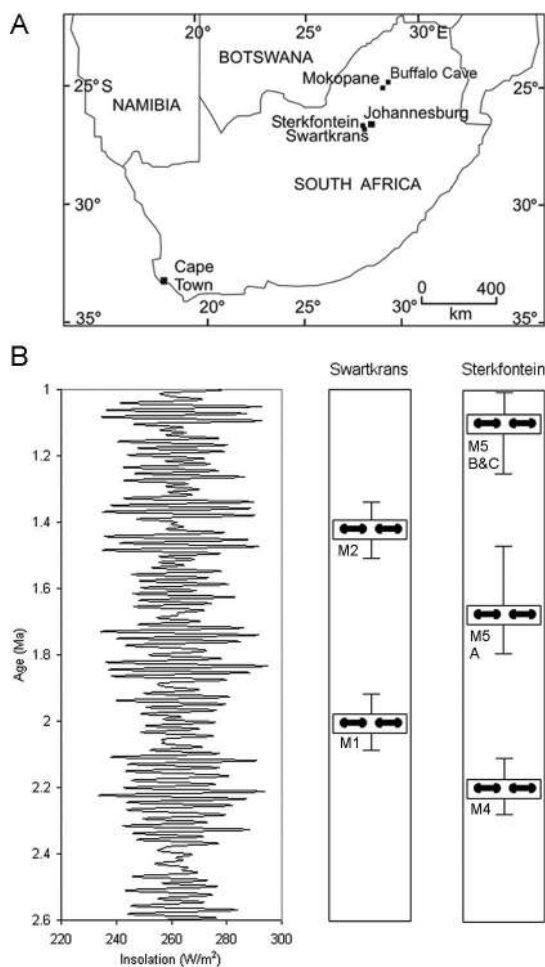


FIGURE 2. A, Localities of South African faunal assemblages and paleoclimatic proxies discussed in the text. B, Chronology of faunal assemblages from Swartkrans and Sterkfontein (Balter et al. 2008; Herries et al. 2009) and July insolation at 24°S during the Plio-Pleistocene (Laskar et al. 2004).

focus of a number of paleoecological and paleoenvironmental analyses in light of their paleoanthropological significance (e.g., Vrba 1980; Reed 1997, 1998; Sponheimer et al. 1999; Lee-Thorp et al. 2000, 2007; O'Regan and Reynolds 2009). Key to these paleoenvironmental reconstructions is the assumption that the faunal deposit in question closely resembles the once living fauna, at least with respect to the parameter being studied. However, faunal deposits are subject to a variety of biases that may affect the "biological fidelity" of the deposit—these include transport bias (including predator accumulation), differential destruction, and time-aver-

aging (Kidwell and Behrensmeier 1993). Taphonomic studies of these faunal deposits have addressed taxonomic bias (Soligo and Andrews 2005), carnivore prey-preferences (Pickering et al. 2004a) and carnivore modification (Pickering et al. 2004b). Although it is accepted that all faunal deposits are time- and space-averaged amalgamations of a once living community (Kidwell and Behrensmeier 1993), there has been only a limited discussion of the extent of time-averaging in these deposits (Vrba 1980; Brain 1981; Blackwell 1994; Schwarcz et al. 1994). Brain (1981, 1995) hypothesized that cycles of sedimentation and erosion at Swartkrans represent glacial and interglacial cycles; however, he provided only limited supporting chronological or environmental evidence. Electron spin resonance ages of bovid enamel from Sterkfontein Member 4 indicated a small amount of mixing with Member 5 sediments (Schwarcz et al. 1994); this mixing was later identified and corrected for using sedimentological evidence (Kuman and Clarke 2000).

The South African faunal deposits were accumulated by multiple carnivore taxa including extinct and extant felids, hominins, hyaenids and birds of prey (Pickering et al. 2004b). The presence of multiple carnivore taxa within each faunal deposit and the presence of tooth-marked bones indicate that the caves were inhabited by a succession of bone-accumulating species. Inherent within this model of multiple accumulators, is the assumption that each faunal deposit has undergone a significant degree of time-averaging (O'Regan and Reynolds 2009). With no constraints on the length of time represented, it must be assumed that the deposits represent thousands to tens of thousands of years worth of time-averaging (as is typical for cave deposits [Kidwell and Behrensmeier 1993]). However, recent studies of Plio-Pleistocene climate variability in tropical and subtropical Africa (Ashley 2007; Hopley et al. 2007; Kingston et al. 2007) have clearly demonstrated climatic variability over precessional time scales (~21,000 years). In fact, rainfall amount and vegetation type fluctuate from one extreme to the other every ~10,500 years (half-precessional cycle; Clement et al. 2004).

In the light of these high-resolution paleoclimate proxies, it is prudent to consider the possibility that some of the faunal deposits accumulated during more than one climatic state to become both time-averaged and climate-averaged faunal deposits. In this study we use high-resolution paleoclimate records from South Africa (Hopley et al. 2007) and the contemporaneous stable isotope measurements of fossil tooth enamel (Lee-Thorp et al. 2007) to investigate the climatic fidelity of the South African faunal deposits.

### Climate-Averaging under Orbitally Forced Climate Change

Orbital forcing controls the frequency of climate change in terrestrial and marine environments, including the migration of ice sheets and changes in global sea level. During the Plio-Pleistocene, ice sheets occupied much of the high- and midlatitude continental regions, either continually or during glacial periods. During the warmer interglacial periods, mammal species were able to colonize these lands, prior to their exclusion during the ice advance of glacial periods. Therefore, most of the Plio-Pleistocene faunal deposits of northern Europe and North America were formed during interglacial or transitional episodes. The ice sheets acted as physical and temporal barriers, resulting in a minimal climatic-averaging of the faunal assemblages.

Tropical and subtropical regions are affected by the precessional cycle primarily through the forcing of total and seasonal rainfall, and secondarily through the vegetation response to rainfall variability (Clement et al. 2004). Unlike mid- and high-latitude regions, the Tropics and subtropics are suitable for occupation by broadly similar mammal communities throughout the entire orbital cycle. It is likely that mammal communities responded to the precessional cycles through migration with the predominant rainfall regimes and vegetation types or through alteration of population size and community structure. This would have resulted in woodland-dominated communities during the high-rainfall extreme of the precessional cycle to savanna-dominated com-

munities during the low-rainfall extreme of the precessional cycle (e.g., Vrba 1995).

As discussed by Maslin and Christensen (2007), the ~21,000 year cycle of eccentricity modulated precession (Fig. 2) has had a significant effect on the climate of tropical regions throughout the Plio-Pleistocene. This can be demonstrated both theoretically (Laskar et al. 2004) and through paleoclimatic evidence (Trauth et al. 2003; Cruz et al. 2005; Hopley et al. 2007). Change in rainfall over precessional cycles was of significant magnitude to force African vegetation change (Hopley et al. 2007) and most likely faunal dynamics (Bobe et al. 2002) throughout the Plio-Pleistocene. Other forcing factors of the tropical climate system, such as changes in ocean circulation or tectonic uplift, are manifested as discrete events or unidirectional trends which either perturb or overlay the precessional oscillations (Maslin and Christensen 2007; Hopley et al. 2007), but do not dampen the precessional signal.

The dominance and regularity of the precessional cycle in tropical paleoclimate records enable us to be confident in our expectation of precessional variability in paleoenvironmental proxies derived from faunal deposits. The likelihood of observing precessional variability within a faunal deposit is dependent on the time resolution of the deposit, which can range from hundreds to tens of thousands of years (Kidwell and Behrensmeyer et al. 1993). Given the overlap between the estimated time-averaging and the ~10,500 years between precessional extremes (half-precessional cycle), it is necessary to explore the consequences of precessional climate variability on the composition and characteristics of faunal assemblages (Fig. 1). Identification of climate-averaging in a faunal assemblage will have consequences for the interpretation of faunal structure, species diversity, and paleoecological reconstructions.

The schematic paleoclimate curve of Figure 1A represents two climatic cycles recorded by a paleoclimate proxy sampled at regular intervals over time. Figures 1B and 1C illustrate variation in the same paleoclimate proxy when a hypothetical sequence of

faunal deposits has accumulated over a period of time equal to one-eighth and one-half of a climatic cycle respectively. As illustrated in Figure 1, there are three main consequences of the accumulation of terrestrial faunas under an oscillating climate:

1. With increasing time-averaging, the intra-deposit variance will increase until the duration of time-averaging matches or exceeds the duration of one-half of the climatic oscillation. The degree of time-averaging will vary slightly depending on which intervals of the climatic cycle are sampled.
2. With increasing time-averaging, the inter-deposit variance will decrease until the mean value for each deposit approaches that of the mean climate proxy value.
3. When time-averaging equals or exceeds the duration of a half-oscillation, the intra-deposit values are likely to display a bimodal distribution.

Using these predictions of time-averaging under an oscillating climate, it is possible to assess the degree to which the South African faunal deposits are climate-averaged with respect to precessional variability.

### Stable Isotopes in Teeth as a Paleoenvironmental Proxy

The South African Plio-Pleistocene faunal deposits have been the focus of a number of detailed studies of carbon and oxygen isotope paleoecology (e.g., Sponheimer and Lee-Thorp 1999; Lee-Thorp et al. 2000, 2007). All taxa and guilds of the faunal deposits have been studied, including micromammals (Hopley et al. 2006), primates including hominins (Lee-Thorp et al. 1989; Sponheimer et al. 2005), herbivorous macromammals (Lee-Thorp et al. 2000) and carnivores (Lee-Thorp et al. 2000; Lee-Thorp et al. 2007). These studies have provided insights into paleodietary behaviors (e.g., Sponheimer et al. 1999) and to a lesser extent, the local paleoenvironment (e.g., Luyt et al. 2003; Lee-Thorp et al. 2007).

### Carbon Isotopes in Fossil Herbivores

Carbon isotope measurements have illuminated subtleties in the dietary preferences of

extinct organisms, often expanding on interpretations made by ecomorphologic analysis alone (e.g., Sponheimer et al. 1999). A secondary application of this work has been to apply stable isotope measurements in herbivore teeth to paleoenvironmental reconstruction. Luyt and Lee-Thorp (2003) and Lee-Thorp et al. (2007) have used the proportions of C<sub>4</sub> grazing bovids to C<sub>3</sub> browsing bovids to produce an index for the percentage of grasslands over time during the Plio-Pleistocene. Herbivore anatomical constraints restrict particular species to specific dietary types with negligible opportunities for dietary adaptation in the face of changing environments. On the basis of  $\delta^{13}\text{C}$  analysis, each herbivore individual can be categorized as belonging to a grazing, browsing, or mixed-feeding species. Taking the fauna as a whole, the proportion of grazers to browsers can be used to indicate the proportion of grassland to woodland in the local environment (after allowing for taphonomic biases such as predator-prey preferences and collection bias). Although each isotopic measurement represents at most a few years of enamel growth, the paleovegetation proxy is based on the proportion of grazers and browsers within the entire faunal deposit and is therefore limited to the temporal resolution of the deposit itself. A  $\delta^{13}\text{C}$  measurement of herbivore enamel taken in isolation reflects the individual's highly selective dietary preferences over a period of a few years, but cannot be used to determine the proportion of vegetation types within the local environment during the period of enamel formation.

### Carnivore Enamel $\delta^{13}\text{C}$ as a Paleovegetation Proxy

Stable isotope analyses of fossil carnivore assemblages have the potential to offer more paleoenvironmental information than analyses of fossil herbivores. The principles of the carnivore carbon isotope paleovegetation proxy are outlined below:

*Carnivores as Ecological Integrators.*—Ecological theory suggests that organisms at higher trophic levels act as integrators, linking lower pathways in space and time (de Ruiter et al. 2005). Primary-producer tissue reflects an

integration of the environmental conditions over the time of tissue growth. Herbivores feed upon numerous primary producers, and carnivores ingest tissues from multiple herbivores. Hence, stable isotope values derived from organisms at higher trophic positions may effectively increase sample size (Bump et al. 2007), thereby reducing variation (i.e., a carnivore represents multiple herbivores, which in turn represent many primary producers). This principle has been successfully tested using stable isotope ecology of the North American grey wolf (Bump et al. 2007) and South African savanna-dwelling carnivores (Codron et al. 2007).

*Carnivores as Dietary Generalists.*—Carnivores will select their prey on the basis of prey availability, size, abundance, and catchability (Hayward and Kerley 2005; Balme et al. 2007; Cooper et al. 2007). Carnivores are able to change their preferred prey species as prey abundance or environmental conditions change (Bodendorfer et al. 2006). Because carnivores are primarily interested in the abundance and size of their prey, and not the dietary preference of their prey, they will readily consume both grazing and browsing herbivores in a mixed savanna-woodland environment (Radloff and Du Toit 2004). Similarly, in a woodland-dominated environment, carnivores will tend to prey on the more abundant browsing herbivores. Despite evidence for some species-specific dietary preferences among the African carnivore guild (e.g., Balme et al. 2007; Cooper et al. 2007), the ecological integrator model tends to hold true among living carnivores (Codron et al. 2007). In addition, Reed (1997) has demonstrated that modern carnivore-accumulated death assemblages can be used to faithfully reconstruct the vegetation types within the locality, irrespective of the habitats present or the accumulating carnivore species.

*Temporal Resolution of the Carnivore Paleovegetation Proxy.*—Following the model of carnivores as ecological integrators (Bump et al. 2007), it is possible to estimate the period of time over which a carnivore  $\delta^{13}\text{C}$  measurement is integrated. A typical stable isotope measurement has a minimum thickness of

1.5 mm in the direction of enamel growth. Depending on the teeth selected for isotopic analysis, this represents between 6 months and 18 months of enamel formation (Hillson 1986) during which the carbon isotopic composition of each herbivore prey specimen is accumulated. In addition, each item of prey represents in excess of one year's worth of primary consumption. We therefore estimate that the  $\delta^{13}\text{C}$  value of an individual carnivore's tooth enamel represents between one and five years worth of ecological integration.

### Stratigraphic and Taphonomic Context of South African Cave Deposits

Identification of individual deposits within the South African cave infills can be problematic owing to similar sedimentological characteristics, a lack of a horizontal depositional sequence, and mixing of deposits through decalcification and slumping. However, sedimentological, faunal, or archaeological markers can be used to determine the spatial and temporal relationships of infills found with the same cave systems (Kuman and Clarke 2000; Lockwood and Tobias 2002). Carnivore involvement in the accumulating process is inferred from damage marks on bones and whole carcass deposition. Additional evidence includes carnivore coprolites and carnivore tooth marks (Brain 1993). A mosaic of bone-accumulating agents is evident in each faunal assemblage, including denning felids and hyaenids (de Ruiter 2004). Although each faunal assemblage analyzed in this study has probably undergone slightly different taphonomic histories, the broadly similar accumulation processes enables comparison between assemblages.

*Sterkfontein Member 4.*—This deposit is considered to have accumulated through the infilling of a large underground chamber along a talus slope (Partridge and Watt 1991). Limited horizontal strata occur toward the northern extreme of the breccia, at the rear of the Member 4 cave. Fragments of fossil wood are found only in the southern half of the infill, proximal to the cave entrance at this time (Kuman and Clarke 2000). Member 4 is characterized by the absence of in situ stone tools, the absence of faunal elements associ-

ated with drier climates, such as *Equus*, *Pedetes*, and *Struthio*, and a fauna and flora indicating a more wooded environment (e.g., the bovid *Makapania broomi* and fossil wood). Pickering et al. (2004a) have demonstrated that large carnivores played a role in the accumulation of the Member 4 hominid assemblage, as evidenced by carnivore tooth marks and patterns of skeletal-part representation.

*Sterkfontein Member 5.*—Following the deposition of Member 4, there was a massive collapse of the infill into lower chambers, creating cavities that were subsequently infilled by later Member 5 breccias (Kuman and Clarke 2000). Kuman and Clarke (2000) were able to divide the majority of the Member 5 faunal assemblage into the older Unit B with Oldowan stone tools and the younger Unit C with Acheulean stone tools. Localized contamination through solution pockets is seen in the top 20 feet of Member 5 East; elsewhere the Member 5 breccia is highly calcified and does not suffer the problems of decalcification. The Unit B Oldowan infill resulted primarily from a death-trap situation in which animals fell down a shaft into the cave; a small proportion of the assemblage accumulated through hillwash. The Unit C Acheulean deposits were accumulated by carnivores, with an additional component of hillwash that was responsible for bringing artifacts into the cave. All the carnivore specimens that have been analyzed for stable isotope analysis are listed as Member 5 (Luyt 2001; Lee-Thorp et al. 2007), without subdivision into Unit B or Unit C. Therefore of the four faunal assemblages investigated in our study, only Sterkfontein Member 5 can be assumed to be a temporally mixed assemblage on the basis of prior stratigraphic information.

*Swartkrans Member 1, Hanging Remnant.*—The Hanging Remnant is an isolated mass of breccia, clinging to the north wall of the cave, undercut along its entire length by an erosional space that was later filled by younger sediments (Brain 1993). It originally rested on a lower and older deposit that had slid downslope, known as Member 1, Lower Bank. The main paleontological sample from

the Hanging Remnant was derived from the Broom/Robinson excavations between 1948 and 1953, and it is from this collection that the carnivore stable isotope measurements were taken (Lee-Thorp et al. 2000). Definitive leopard canine punctures in an early hominid calotte from the Hanging Remnant indicate leopard involvement in the accumulation of the assemblage (Brain 1970). Pickering et al. (2008) have confirmed the near-exclusive leopard predation signal in Swartkrans Member 1.

*Swartkrans Member 2.*—Following the deposition of Swartkrans Member 1, a period of erosion displaced decalcified sediment into lower levels of the cave and created space for the Member 2 infill (Brain 1993). Pickering et al. (2008) provide evidence for a mixed leopard and hyaenid signal in Member 2, representing multiple phases of carnivore predation.

## Methods

### Carnivore Enamel $\delta^{13}\text{C}$ Data Set

All published and unpublished carnivore enamel  $\delta^{13}\text{C}$  data for the four faunal assemblages studied (Swartkrans Members 1 and 2 and Sterkfontein Members 4 and 5) were collated into one data set. Data were sourced from Lee-Thorp et al. (1997, 2000, 2007) and Luyt (2001).  $\delta^{13}\text{C}$  mean, range, and frequency distribution were plotted for individual species within individual faunal assemblages (*P. leo* Sterk M5, *P. pardus* Swart M1, *C. nitidula* Sterk M4); individual species across multiple faunal deposits (all species); multiple species within individual faunal deposits (all deposits) and for the data set as a whole. These results were then compared with the two time-averaging scenarios derived from the modeled carnivore enamel  $\delta^{13}\text{C}$  time series for the Plio-Pleistocene.

### Modeling Herbivore Carrying Capacity, Carnivore Diets, and Time-Averaging

*Grazing and Browsing Capacity.*—The ecological grazing and browsing capacity for herbivores within a habitat is the maximum number of grazers and browsers that a given area of land can sustain, based on the

biophysical resources of the area. Grazing capacity for herbivores reflects the ecological production potential of the grazeable portion of a homogeneous unit of vegetation and represents the area of land (ha) required to maintain a single Grazer Unit (GU) over an extended number of years without deterioration of the vegetation or the soil. Following the methodology of Bothma et al. (2004), the equation for calculation of the carrying capacity of grazing herbivores in modern-day South Africa can be extended into the Plio-Pleistocene:

$$\begin{aligned} \text{GU}/100 \text{ ha} \\ &= 0.547 \times ((c + (r - l) \times 0.23) \\ &\quad \times a \times f \times (\log_{10}g - 1)^{0.4}) \quad (1) \end{aligned}$$

where:

GU = grazer units; 1 GU in South Africa is commonly taken as a blue wildebeest (*Connochaetes taurinus*) with a mass of 180 kg because it is an abundant, large herbivore with a mainly grazing diet. The grazing capacity for herbivores is expressed as GU/100 ha.

$c$  = the range condition index, a quantitative measure of the ecological condition of the herbaceous layer (grazing value, palatability, and productivity in phytomass), reflecting its ability to support grazing herbivores. The mean range condition for seven wildlife ranches in the Limpopo province of South Africa is 39% (Bothma et al. 2004). A nominal range condition of 40% was chosen for the Plio-Pleistocene of South Africa and no attempt was made to reflect changes in range condition during precessional cycles.

$r$  = the mean annual rainfall over the past two years (mm). In the absence of annual rainfall data for the Plio-Pleistocene, a random value between  $l - 50$  and  $l + 50$  was selected to reflect the essentially random nature of annual rainfall variability in modern-day Southern Africa.

$l$  = the long-term annual rainfall. The oxygen isotope record for the Plio-

Pleistocene of Buffalo Cave predominantly reflects rainfall amount in South Africa (Hopley et al. 2007). Calibration of the Buffalo Cave  $\delta^{18}\text{O}$  record in terms of rainfall amount was based on the precessional variability in rainfall amount determined by Partridge et al. (1997)—from 800 mm at insolation maxima to 400 mm at insolation minima during the late Pleistocene.

$a$  = a topography index of accessibility—the degree of accessibility of the habitat to plains wildlife on a scale of 0.1–1.0, with 1.0 = fully accessible. Carnivores accumulating bones at Sterkfontein and Swartkrans had access to plains wildlife over approximately 50 km<sup>2</sup> centered on the cave sites. Taken as a whole, we assume a high topographic index of accessibility (0.9) for this locality in the Plio-Pleistocene.

$f$  = a fire factor on a scale of 0.8–1.0, with 0.8 = recent fire and 1.0 = absence of fire. For the Plio-Pleistocene, a random number between 0.8 and 1.0 was selected to encompass the entire range of fire factors.

$g$  = the percentage of grass cover. In subtropical savannas, the percentage of grass cover is synonymous with the percentage of C<sub>4</sub> vegetation, which has been determined for the Plio-Pleistocene of South Africa by  $\delta^{13}\text{C}$  analysis of speleothems (Hopley et al. 2007).

The browsing capacity reflects the area of land (ha) required to maintain a single Browser Unit (BU) over an extended number of years without deterioration of the vegetation or the soil. Following the methodology of Bothma et al. (2004), the equation for calculation of the carrying capacity of browsing herbivores in modern-day South Africa can be extended into the Plio-Pleistocene:

$$\text{BU}/100 \text{ ha} = (b \times m \times a)/r \quad (2)$$

where:

BU = browser units; 1 BU in South Africa is commonly taken as a greater kudu



(*Tragelaphus strepsiceros*) with a mass of 140 kg because it is an abundant, large herbivore with a mainly browsing diet. The browsing capacity for wildlife is expressed as BU/100 ha.

$b$  = the percentage of standing browse. In subtropical savannas, the percentage of standing browse is synonymous with the percentage of  $C_3$  vegetation, which has been determined for the Plio-Pleistocene by  $\delta^{13}C$  analysis of speleothems (Hopley et al. 2007).

$m$  = the dry leaf mass of 1% of the standing browse in kg per 100 ha. Various approaches can be taken when estimating the mass of standing browse (Melville et al. 1999) in African savannas. We use the modern-day South African value of 4437 (calculated from Bothma et al. 2004) and assume a similar value for the Plio-Pleistocene.

$a$  = fraction of available browse. It has been widely observed that browsers in Africa use <10% of the standing browse in any area (Bothma et al. 2004). As the majority of prey species accumulated by carnivores at Sterkfontein and Swartkrans were unlikely to access standing browse >2 m tall, we have assumed that on average the Plio-Pleistocene herbivore assemblage would have consumed approximately 8% (0.08) of the available browse (see Bothma et al. 2004).

$r$  = amount of browse required by 1 BU per year in kg. The daily food requirements of a 140 kg greater kudu (used as the BU reference value) is approximately 3% of its body mass (Bothma et al. 2004), such that 1 BU consumes 1533 kg of dry leaf matter per year.

By combining equations (1) and (2) we were able to produce a modeled time series of the percentage of grazers within the Plio-Pleistocene herbivore community.

*Modeling Predator Diet.*—The typical home range for modern-day African predatory carnivores (e.g., lions) and scavenging carnivores (e.g., hyenas) is approximately 50 km<sup>2</sup> (Spong 2002; Boydston et al. 2003). It is

therefore reasonable to assume that the Plio-Pleistocene carnivore species also sourced their herbivorous prey over a similar 50 km<sup>2</sup> home range. Because paleodietary indicators such as carbon isotopes are dependent on the mass of foodstuffs ingested, rather than the number of individuals consumed, it is preferable to determine herbivore biomass rather than grazer and browser units. The grazer and the browser biomass to be expected within a 50 km<sup>2</sup> home range were calculated by multiplying the number of grazing or browsing individuals by their standardized herbivore masses of 180 kg or 140 kg respectively.

The following equation can then be used to predict carnivore enamel  $\delta^{13}C$  from the percentage of grazer biomass:

$$\begin{aligned} \text{Carnivore enamel } \delta^{13}C \\ = -11 + g/10 + r + a \end{aligned} \quad (3)$$

where:

$g$  = percentage of grazer biomass within the herbivore community.

$r$  = a random number representing individual differences in carbon isotope discrimination. Carnivores consuming a homogenous diet will display up to 1.5‰ of  $\delta^{13}C$  variability (Sillen and Lee-Thorp 1994) due to individual physiological and dietary differences. This isotopic variability can be represented by the computation of a random number between -0.75 and +0.75.

$a$  = prey abundance bias. Predators will preferentially select their prey on the basis of prey abundance (Hayward and Kerley 2005; Hayward 2006; Hayward et al. 2006a,b). For the Plio-Pleistocene of South Africa we have created a simplified parameterization of this bias: when  $g = 50$ , the bias is 0; when  $g = 75$ , the bias is 2.5; and when  $g = 25$  the bias is -2.5. We have represented this term by the equation

$$a = (g - 50)/10. \quad (4)$$

*Modeling Time-Averaging.*—The modeled time series of carnivore enamel  $\delta^{13}C$  detailed

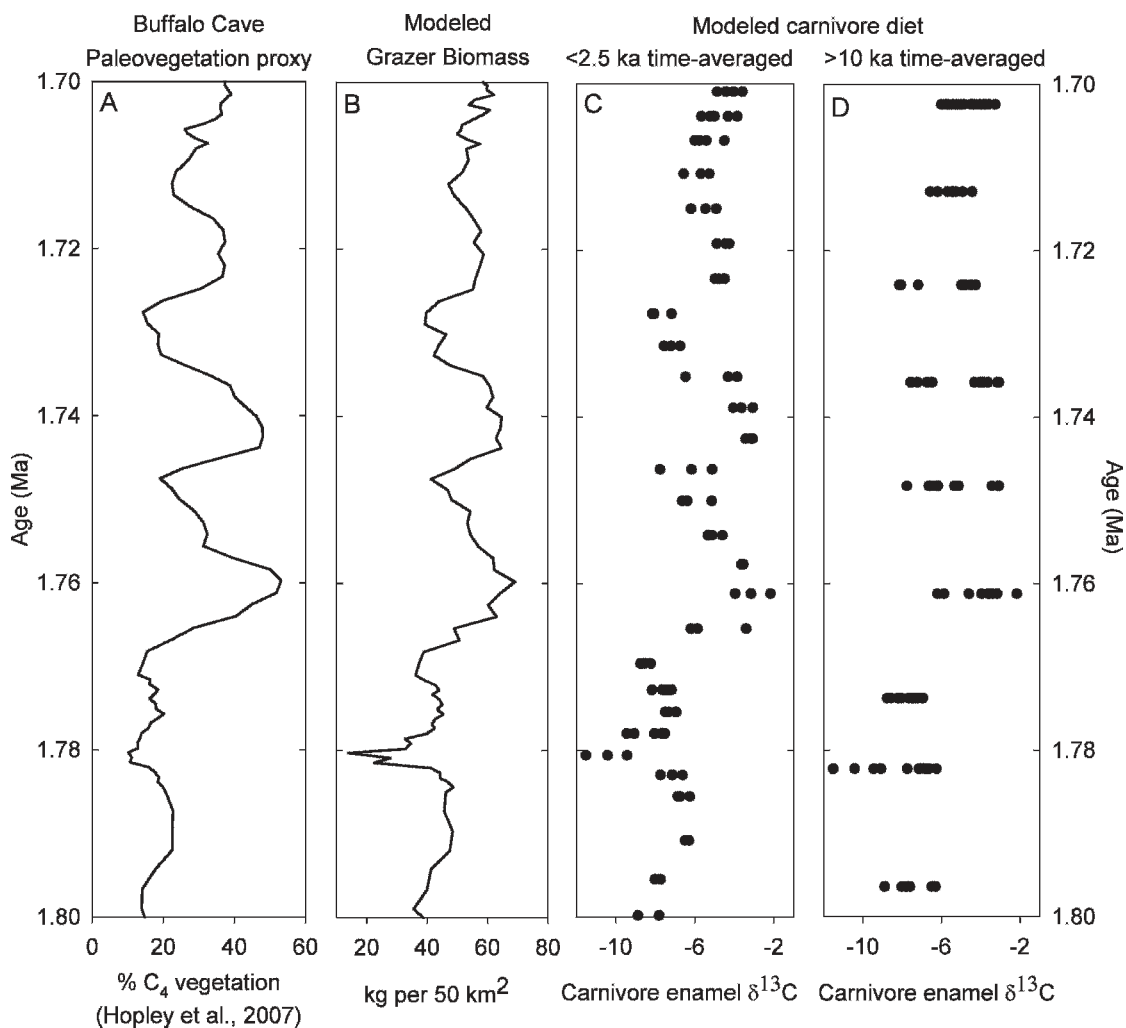


FIGURE 3. Modeling the effects of time-averaging on the environmental fidelity of faunal deposits from South African hominin sites. A, The Buffalo Cave Plio-Pleistocene record of precessionally forced vegetation change in northern South Africa (Hopley et al. 2007). B, Modeled grazer biomass in the Plio-Pleistocene, determined from the carrying capacity calculations of South African savannas in the modern day (Bothma et al. 2004). C, D, Modeled carnivore enamel  $\delta^{13}\text{C}$  values for the Plio-Pleistocene, based on carnivore hunting behaviors in the modern day (Hayward et al. 2007). Time-averaging the carnivore enamel  $\delta^{13}\text{C}$  data at intervals of <2.5 Kyr (C) preserves the key features of the original vegetation record (A). Time-averaging the carnivore enamel  $\delta^{13}\text{C}$  data at intervals of >10 Kyr (D) sees the loss of precessional cyclicity; in addition, there is an amplification of the low-frequency shift in vegetation at 1.77 Ma (Hopley et al. 2007).

above (see Fig. 3) has 500,000 years duration and a temporal resolution of approximately 1000 years. Using this data set as a template, we were able to produce two time-averaged time series—the first averaged every 2500 years (Fig. 3C) and the second averaged every 10,000 years (Fig. 3D). Analysis of modeled  $\delta^{13}\text{C}$  mean, range, and distribution within time intervals and between time intervals was undertaken to assess the degree to which

time-averaging affects the environmental fidelity of carnivore enamel  $\delta^{13}\text{C}$ .

## Results

*Carnivore Dietary Behavior.*—The multimodal and bimodal distribution of  $\delta^{13}\text{C}$  in herbivore and carnivore enamel, respectively, from all four faunal assemblages enables us to distinguish a number of dietary behaviors (see Fig. 4). Individuals within the herbivore-

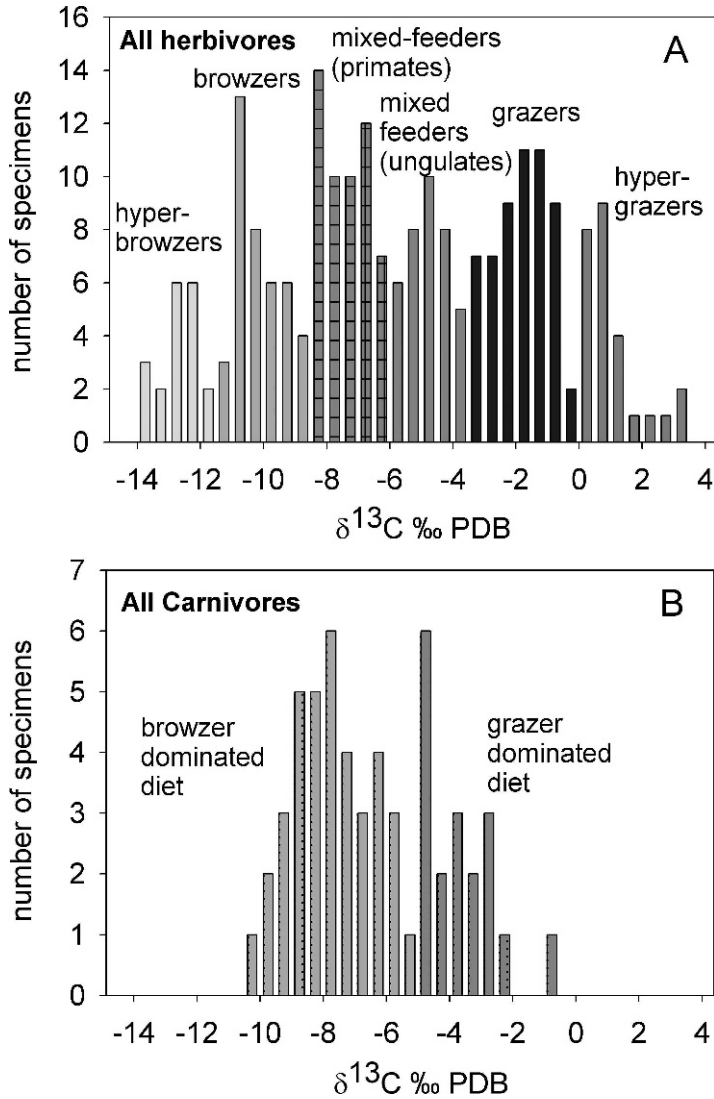


FIGURE 4.  $\delta^{13}\text{C}$  distributions of the different dietary behaviors found within the herbivorous guild (A) (Lee-Thorp et al. 2007) and the carnivorous guild (B) for the four South African assemblages combined (Sterkfontein M4 and M5; Swartkrans M1 and M2).

rous guild can be assigned to the hyper-browser, browser, mixed-feeder (primates), mixed-feeder (ungulates), grazer, and hyper-grazer categories. The bimodal distribution of carnivore  $\delta^{13}\text{C}$  enables individuals within the carnivorous guild to be assigned a browser-dominated diet or a grazer-dominated diet. Using the arguments outlined above, we interpret the browser (grazer)-dominated diet as indicative of a carnivorous individual living within a woodland (grassland)-dominated environment. Taking the carnivore data set as a whole, it is evident that the browser-

dominated diet, and by implication the available browse, is slightly more common than grass cover, in agreement with other paleovegetation proxies from South Africa (Hopley et al. 2007; Lee-Thorp et al. 2007).

*Enamel  $\delta^{13}\text{C}$  Variability within Species.*—Analysis of the carnivore  $\delta^{13}\text{C}$  data set at the species level is restricted to the three species that have five or more specimens analyzed from one faunal deposit: *P. pardus* from Swartkrans Member 1; *P. leo* from Sterkfontein Member 5; and *C. nitidula* from Sterkfontein Member 4. The  $\delta^{13}\text{C}$  values of *P. pardus* and *P. leo* have ranges of

7.6‰ and 7.7‰ respectively, indicating that variability within a single species can equal the variability observed for a multi-species assemblage (see Figs. 5, 6). For both species, some individuals were almost exclusively consuming browsing herbivores whereas other individuals of the same species were almost exclusively consuming grazing herbivores. If either of the two faunal deposits were considered to represent one contemporaneous community, then it would be necessary to invoke extreme dietary partitioning between individuals of different ages or sexes. A far more likely explanation is that each faunal deposit contains individuals from both grass-dominated and woodland-dominated environments. The third species, *C. nitidula*, has a lower  $\delta^{13}\text{C}$  range of 4.4‰, with no individuals consuming an entirely  $\text{C}_4$  grass dominated diet. As discussed below, this suggests that *C. nitidula* did not live in the surroundings of Sterkfontein during grassland-dominated episodes—instead it was restricted to periods of the precessional cycle when there was greater woody cover.

*Enamel  $\delta^{13}\text{C}$  Variability within Faunal Assemblages.*—As demonstrated in Figure 6, there is a large range in intra-deposit carnivore  $\delta^{13}\text{C}$  (in excess of 5.9‰) for each of the four faunal assemblages studied. Each deposit contains individuals that consumed an exclusively  $\text{C}_3$  diet and individuals that consumed an exclusively  $\text{C}_4$  diet (Fig. 6). None of the faunal deposits have  $\delta^{13}\text{C}$  values that lie within just one of the predicted distributions for the two vegetation end-members. The most likely explanation for these highly variable carnivore  $\delta^{13}\text{C}$  values is that individuals from all phases of the precessional cycle are represented. Comparison with the modeled carnivore  $\delta^{13}\text{C}$  distributions enables the fossil individuals to be placed within either the woodland- or savanna-dominated phases of the precessional cycle.

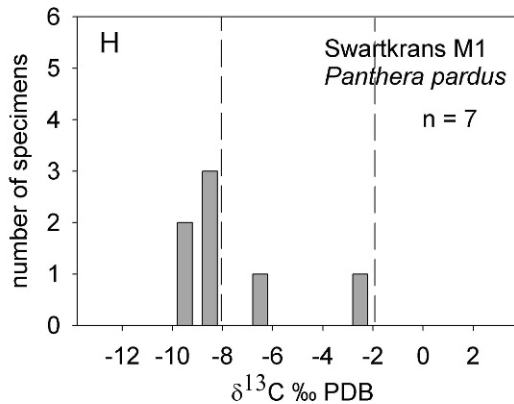
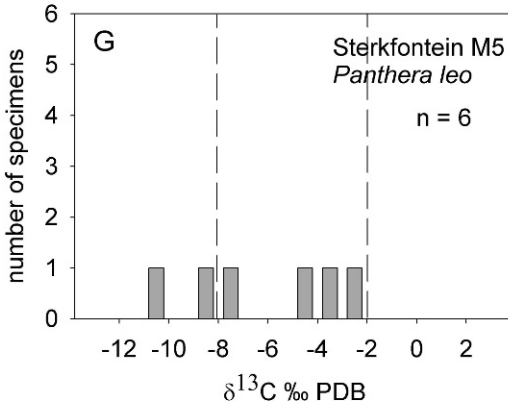
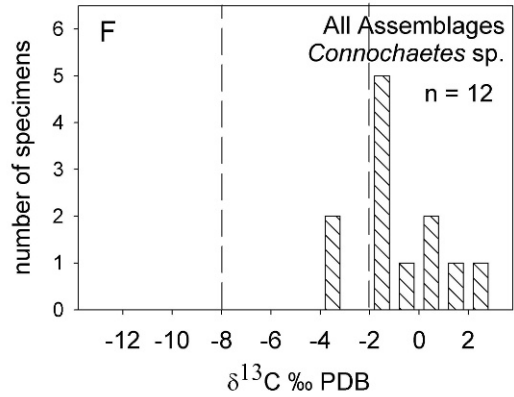
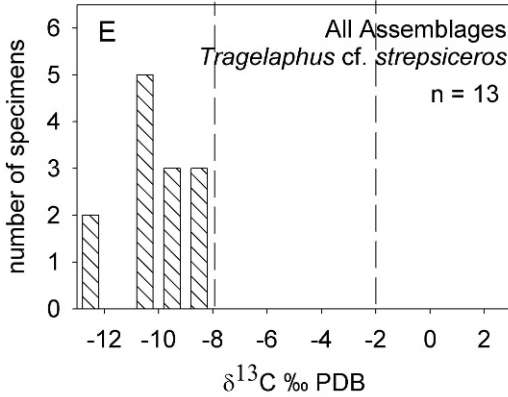
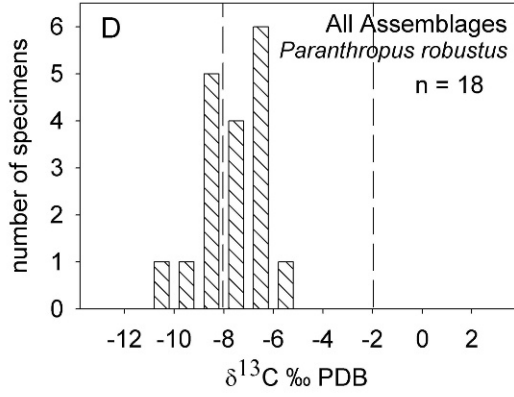
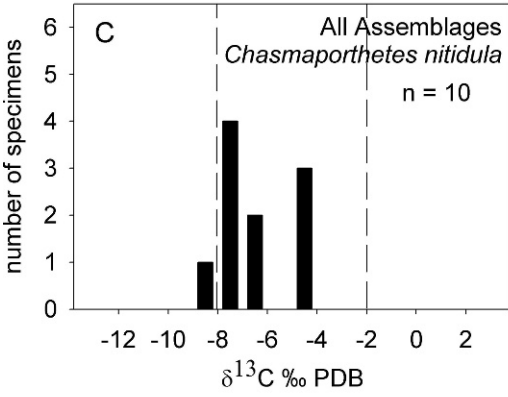
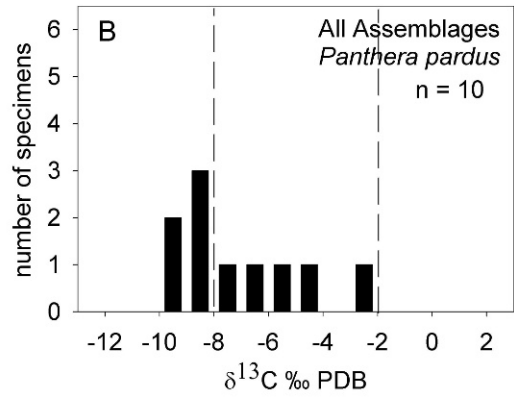
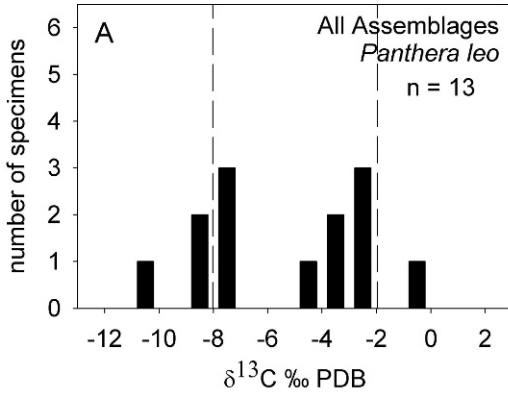
Alternatively, it could be argued that the wide  $\delta^{13}\text{C}$  distributions shown in Figure 6 represent wide-ranging dietary choice in a contemporaneous carnivore community. In a continuously mixed environment supporting 50% browsers and 50% grazers, it would be theoretically possible to support such a wide range in carnivore diet, as individual carnivore

species could opt to specialize on either grazing or browsing herbivore species. However, as demonstrated in Figure 3, we know that the vegetation and therefore the herbivore community in the Plio-Pleistocene varied from grass-dominated to woodland-dominated end-members, with only short periods when browsers and grazers were equally available. However, at times when either grazers or browsers dominated the herbivore guild (~80% of each precessional cycle; see Fig. 3), all predators would be obliged to share the same isotopically homogenous herbivore resource and would have similar dietary  $\delta^{13}\text{C}$  inputs.

*Enamel  $\delta^{13}\text{C}$  Variability Between Faunal Assemblages.*—As shown in Figure 6, the mean  $\delta^{13}\text{C}$  carnivore enamel value varies from  $-7.4$  for Swartkrans M1 to  $-3.7$  for Swartkrans M2. Taking the four faunal deposits as a whole, the mean  $\delta^{13}\text{C}$  value of carnivore enamel is  $-5.9$ ‰, with a standard deviation of 1.6‰. Swartkrans M2 is the most  $\text{C}_4$  grass dominated of the four assemblages; only one carnivore is securely within the predicted distribution for individuals living during a  $\text{C}_3$ -browse-dominated episode. Swartkrans M2 is the youngest of the faunal assemblages studied (Fig. 2) and is the only deposit to be entirely younger than the 1.7-Ma stepwise shift to more open savanna environments (Fig. 3) (Hopley et al. 2007). With a carnivore enamel  $\delta^{13}\text{C}$  range similar to that of the other three South African assemblages, it is possible that Swartkrans M2 is sampling individuals from all phases of one or more precessional cycles, albeit under a more grassland-dominated environment.

## Discussion

It is highly unlikely that the faunal assemblages at Sterkfontein and Swartkrans were accumulated under a constant climatic regime, as implied by previous authors (e.g., Reed 1997; Susman et al. 2001; Lee-Thorp et al. 2000; Sponheimer et al. 2005; Grine 2005). Instead, the evidence presented in this study indicates that each member is an amalgamation of individuals from the grass-dominated and the woodland-dominated extremes of the precessional cycle, accumulated over a period in excess of ~7000 years (one-third of a precessional cycle). As shown in Table 1, the stable



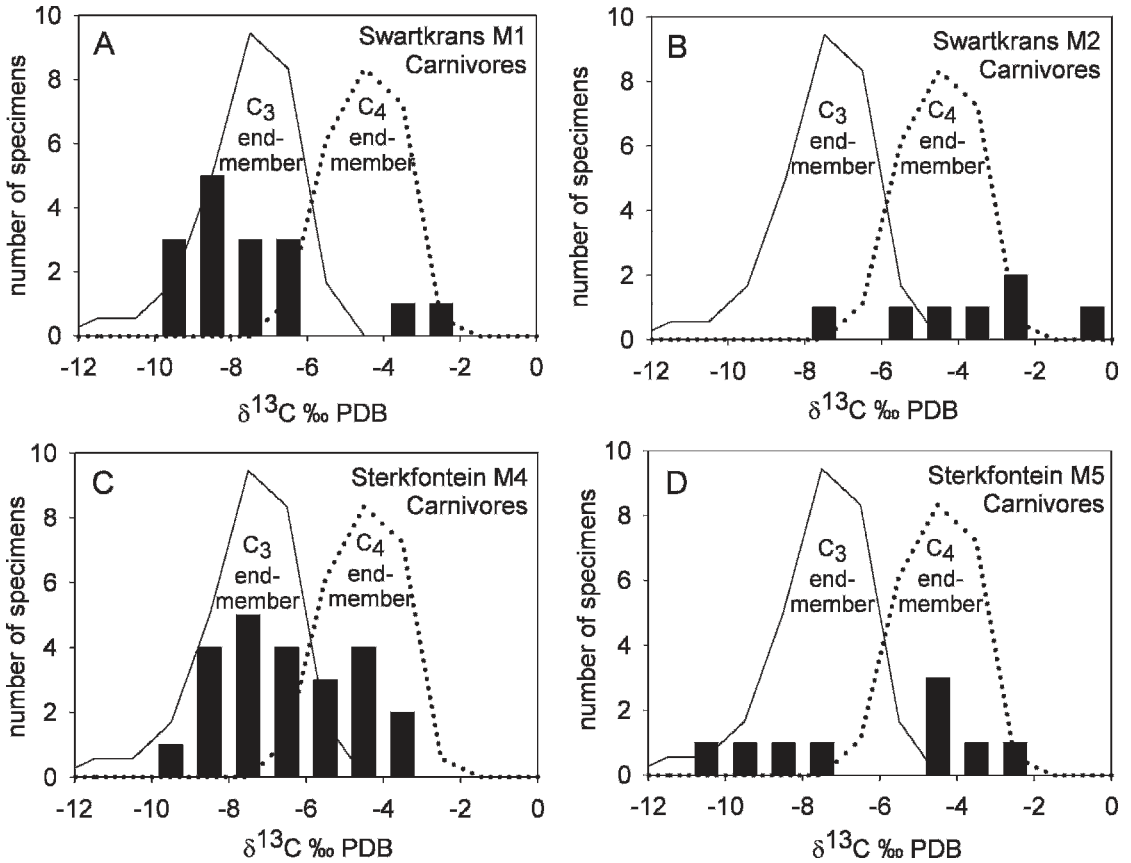


FIGURE 6.  $\delta^{13}\text{C}$  distributions of carnivore enamel for each faunal assemblage compared with modeled distributions for the  $\text{C}_3$ -dominated and the  $\text{C}_4$ -dominated phase of the precessional cycle. Each faunal assemblage contains carnivore individuals with  $\delta^{13}\text{C}$  values that lie within both of the modeled distributions, suggesting they are derived from more than one phase of the precessional cycle.

isotope evidence can be used to associate some carnivore species with particular phases of the precessional cycle. The reinterpretation of the taphonomy of these deposits has a number of implications for our understanding of the paleoecology of the faunal assemblages.

#### Paleoecological Consequences

*Sympatry.*—The identification of apparent sympatry among fossil hominin species in South Africa (Grine 2005; Curnoe and Tobias

2006) and East Africa (Spoor et al. 2007) is considered suggestive of either competition or niche differentiation between hominin species (Pickering 2006). Theoretical preference for the niche differentiation hypothesis (Summers and Neville 1978; Stanford 2006) has seen renewed interest in the identification of dietary specializations among contemporaneous hominin species (Pickering 2006).

The co-occurrence of closely related species within individual faunal assemblages (e.g., *P.*

FIGURE 5. Distribution of  $\delta^{13}\text{C}$  measurements for individual carnivore species (A–C) compared with typical ungulate and primate species (D–F), using data from all four faunal assemblages combined (Sterkfontein M4 and M5, and Swartkrans M1 and M2). The carnivore species tend to show broader  $\delta^{13}\text{C}$  distributions than the ungulates and primates, indicating a variable dietary input. G, H,  $\delta^{13}\text{C}$  distributions of carnivore species from individual faunal assemblages;  $\delta^{13}\text{C}$  distributions show a range similar to the  $\delta^{13}\text{C}$  distributions of the combined faunal assemblages. Vertical lines indicate division between a purely  $\text{C}_3$  diet ( $< -8\text{‰}$ ), a mixed diet ( $-8\text{‰}$  to  $-2\text{‰}$ ) and a purely  $\text{C}_4$  diet ( $> -2\text{‰}$ ). Black bars, carnivore species, combined assemblages; gray bars, carnivore species, individual assemblages; hatched bars, ungulate and primate species, combined assemblages.

TABLE 1. Summary of dietary range observed for each carnivore species and their inferred occurrence during the three different phases of the precessional cycle. Ticks indicate presence, crosses indicate absence, and question marks indicate insufficient evidence. Predation of predominantly grass-consuming herbivores is more common among the extant carnivore species, indicating a broader dietary behavior among these species.

Carnivores	Presence within phases of precessional cycle		
	Grass-dominated ( $\delta^{13}\text{C} > -3.5$ )	Mixed $\delta^{13}\text{C} =$ $-7$ to $-3.5$ )	Woodland-dominated ( $\delta^{13}\text{C} < -7$ )
Extant species			
<i>Panthera leo</i> (n = 13)	✓	✓	✓
<i>Crocuta crocuta</i> (n = 4)	✓	✓	✓
<i>Panthera pardus</i> (n = 10)	✓	✓	✓
<i>Parahyena brunnea</i> (n = 2)	?	✓	✓
<i>Canis mesomelas</i> (n = 4)	?	✓	?
Extinct species			
<i>Dinofelis barlowi</i> (n = 3)	?	✓	✓
<i>Homotherium</i> sp. (n = 4)	×	×	✓
<i>Chasmaporthetes nitidula</i> (n = 10)	×	✓	✓
<i>Chasmaporthetes silberbergi</i> (n = 2)	?	✓	?
<i>Pachycrocuta brevirostris</i> (n = 2)	?	✓	✓
<i>Megantereon whitei</i> (n = 1)	?	?	✓

*robustus* and early *Homo* in Swartkrans M1 and M2 [Grine 2005; Curnoe and Tobias 2006]) has been used as evidence of sympatry in South Africa. Their relative abundance has also been used to suggest differences in vulnerability to leopard predation (Susman et al. 2001). The co-occurrence of two taxa within a faunal assemblage is not *ipso facto* evidence of sympatry; geographical or temporal separation must be considered. Geographical separation is unlikely to exceed the limits of the accumulating agent (e.g., the carnivore home range), so within a  $\sim 50$  km<sup>2</sup> area, it could be possible to support two largely independent hominin populations—one restricted to woodland areas (perhaps riparian), the other restricted to savanna areas. However, given the evidence for similar dietary behaviors in *P. robustus* and early *Homo* (Pickering 2006), this kind of geographical separation seems unlikely. Under a temporal separation scenario, one hominin species would have lived during the woodland-dominated extreme of the precessional cycle, and the other hominin species would have lived during the savanna-dominated extreme of the precessional cycle. Both species would have had access to woodland and savanna resources, although specific foraging behaviors may have been different. Predator accumulation lasting more than  $\sim 7000$  years would have concentrated the two allopatric species within a single

faunal deposit, giving the appearance of sympatry. The evidence presented here cannot prove or disprove the sympatry hypothesis, but it does provide a plausible alternative—that of two temporally distinct hominin species adapted to two different paleoclimatic regimes.

*Community Structure.*—A number of studies have analyzed the community structure of the South African faunal assemblages. The overrepresentation of large primary consumers in the fossil assemblages in comparison with modern-day African mammal faunas (Reed 1997; Soligo and Andrews 2005) has been recognized as a consistent taphonomic bias. Taking this bias into account, Reed (1997, 1998) compared the ecomorphological composition of the fossil assemblages with those of modern-day faunas. For example, at Swartkrans M1, Reed (1997) identified 13.89% fruit and leaf eaters, 5.56% aquatic animals, and 2.78% fresh grass grazers, with the remaining individuals belonging to grazing animals. Reed (1997) suggests that the environment was an open habitat, with riparian woodland and patches of edaphic grassland. In addition, more meat-eating carnivore species are present in the fossil localities than in modern-day communities (Reed 2002; O'Regan and Reynolds 2009), and browsing herbivores are also considered to be overrepresented (Reed 2002). To explain the increased biodiversity observed in the Plio-

cene locality of Makapansgat, Reed (2002) suggested that the productivity of the ecosystem may have been higher in the past. In our opinion, a more parsimonious explanation is that the faunal assemblages are climate-averaged, resulting in assemblages with an artificially increased biodiversity and an unusually broad range of ecomorphologies.

Future work will need to focus on methodologies for identifying the woodland-dominated and savanna-dominated components of the mixed faunal assemblages. Some further insights may be gained through developing areas of stable isotope research (e.g., Levin et al. 2006), or through clarification of predator-prey relationships, as indicated by species-specific tooth marks on herbivore bones (Pickering et al. 2004a,b).

#### Implications for Paleoclimate Reconstruction

The demonstration of climate-averaging in the South African hominin faunal assemblages necessitates the reconsideration of the many studies that have collected paleoecological information from these faunal assemblages. As illustrated in Figure 1, climatically averaged deposits can provide an understanding of the average paleoclimatic conditions experienced during one or more climatic cycles; they are also well suited for studies of low-frequency climatic changes, such as the stepwise shift vegetation observed at 1.7 Ma (Luyt et al. 2003) (Fig. 3D). This study highlights the fact that faunal deposits formed in tropical savanna environments cannot be assumed to represent one fossil community formed under stable environmental conditions. Future studies of time-averaging in other hominin localities in eastern and southern Africa will be required to determine the degree to which climate-averaging is a continent-wide phenomenon.

#### Conclusions

We have demonstrated that tropical and subtropical terrestrial faunal assemblages will undergo climate-averaging if they accumulate over a period of time greater than one-third of a precessional cycle (~7000 years). This degree of time-averaging is well within the expected

range for many terrestrial bone accumulations (Behrensmeier et al. 2000), indicating that climate-averaging may be a common phenomenon at low-latitude localities. Given the long history of precessional forcing of monsoon rainfall intensity at low latitudes, from the late Quaternary (e.g., Cruz et al. 2005) to the Mesozoic (e.g., Beckmann et al. 2005) and beyond, we suspect that much of the tropical terrestrial vertebrate record accumulated under rapidly oscillating rainfall and vegetation regimes. This has a number of implications for the paleoecological fidelity of many tropical and subtropical fossil assemblages.

Using  $\delta^{13}\text{C}$  of carnivore enamel as a paleovegetation proxy, we investigated climate-averaging in four Plio-Pleistocene faunal assemblages from South Africa. By comparing measured values of carnivore enamel  $\delta^{13}\text{C}$  with values predicted from known vegetation variability in the Plio-Pleistocene of South Africa, we were able to assess the degree to which climate-averaging had taken place. We conclude that carnivore enamel  $\delta^{13}\text{C}$  can be considered an integration of the local vegetation signal (through the consumption of numerous herbivorous prey species) over a period of just a few years. Swartkrans M1 and M2 and Sterkfontein M4 and M5 all displayed a range of carnivore  $\delta^{13}\text{C}$  consistent with accumulation under both the woodland-dominated and grassland-dominated extremes of the precessional cycle, indicating that each deposit took more than ~7000 years to accumulate. This degree of climate-averaging has implications for existing models of hominin sympatry and for estimates of biodiversity in the Plio-Pleistocene of South Africa. Future analyses of hominin paleoecology in Africa need to consider the degree to which faunal assemblages have been climatically and temporally mixed.

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